

云南曲靖志留纪罗德洛世 真盔甲鱼类一新属¹⁾

朱 敏 刘玉海 贾连涛 盖志琨

(中国科学院古脊椎动物与古人类研究所,脊椎动物进化系统学重点实验室 北京 100044)

摘要:记述了云南曲靖潇湘区关底组(志留系罗德洛统)真盔甲鱼类一新属、新种——长孔盾鱼(*Dunyu longiforus* gen. et sp. nov.)，丰富了以梦幻鬼鱼为代表的潇湘脊椎动物群的组成。该新属具真盔甲鱼科的鉴别特征：后眶上管和中背管二者连续过渡，后端两侧辏合呈“U”字形，侧背管仅发出3条侧横管。新属内角缺如，这一特征过去在真盔甲鱼科中仅见于真盔甲鱼属。新属区别于真盔甲鱼属的主要特征有：角向后方延伸，呈棘状或叶状；头甲最宽处位于角末端之前，宽长比小于1.1；中背孔末端超越眶孔后缘连线。基于对秀山真盔甲鱼头甲标本的重新观察，将秀山真盔甲鱼归入盾鱼属。新种区别于秀山盾鱼(*Dunyu xiushanensis*)的特征有：个体较大，头甲长大于宽；角呈棘状；眶孔位置相对靠前，头甲眶前区与眶后区的长度之比小于0.75；多边形瘤状瘤点，较大，长可超过2 mm。

关键词：云南曲靖，志留纪，盔甲鱼类，真盔甲鱼科，新属

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A NEW GENUS OF EUGALEASPIDIFORMS (AGNATHA: GALEASPIDA) FROM THE LUDLOW, SILURIAN OF QUJING, YUNNAN, SOUTHWESTERN CHINA

ZHU Min LIU Yu-Hai JIA Lian-Tao GAI Zhi-Kun

(Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences Beijing 100044 zhumin@ivpp.ac.cn)

Abstract A new genus and species of the Eugaleaspidiformes (Agnatha: Galeaspidida), *Dunyu longiforus* gen. et sp. nov., is described from the Ludlow (Silurian) Kuanti Formation of Qujing, Yunnan, southwestern China, in association with the oldest near-complete gnathostome *Guizy unoiros* of the Xiaoxiang Vertebrate Fauna. The new genus is most suggestive of *Eugaleaspis* of the Eugaleaspididae by the absence of inner corners, in addition to the diagnostic features of the family, such as only 3 pairs of lateral transverse canals from lateral dorsal canals, and the U-shaped trajectory of median dorsal canals. They differ in that the new genus possesses a pair of posteriorly extending corners, the breadth/length ratio of the shield smaller than 1.1, and the posterior end of median dorsal opening beyond the posterior margin of orbits. *Eugaleaspis xiushanensis* from the Wenlock Huixingshao Formation of Chongqing is re-assigned to *Dunyu*, based on the new examination of the type specimen which shows a pair of posteriorly extending lobate corners and three (instead of four in the original description) pairs of lateral transverse canals. The

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new species differs from *Dunyu xiushanensis* in its large cephalic shield which is longer than broad, spine-shaped corners, anteriorly positioned orbits, the length ratio between preorbital and postorbital portions of the shield less than 0.75, and large polygonal, flat-topping tubercles exceeding 2.0 mm in length.

Key words Qujing, Yunnan; Silurian; Galeaspida, Eugaleaspidiformes, new genus

1 Introduction

The Xiaoxiang Fauna (Zhu et al., 2009), characterized by the early diversification of gnathostomes or jawed vertebrates (Qu et al., 2010), is distributed in the Qujing area, Yunnan, southwestern China. In addition to the oldest near-complete bony fish *Guizy unoiros* (Zhu et al., 2009; Qiao and Zhu, 2010), the Xiaoxiang Fauna or the Kuanti vertebrate assemblage (Zhao and Zhu, 2010) includes agnathans, placoderms, acanthodians and other osteichthyans under study. Here we describe a complete cephalic shield which represents a new form of the Eugaleaspidiformes (Agnatha; Galeaspida), and provides new data on the morphology and taxonomy of the group (Liu, 1965, 1975; Halstead et al., 1979; Janvier, 1984; Pan, 1992; Zhu, 1992; Gai and Zhu, 2005; Gai et al., 2005, 2011; Zhu and Gai, 2006).

2 Systematic paleontology

Subclass Galeaspida Tarlo, 1967

Order Eugaleaspidiformes (Liu, 1965) Liu, 1980

Family Eugaleaspididae (Liu, 1965) Liu, 1980

Dunyu gen. nov.

Etymology From *dun* (Chinese Pinyin), meaning shield, and *yu* (Chinese Pinyin), meaning fish.

Type species *Dunyu longiforus* sp. nov.

Diagnosis Small-to medium-sized cephalic shield with its maximum breadth at a level anterior to corner apex, the breadth/length ratio smaller than 1.1; median dorsal opening extending posteriorly beyond orbits; corner extending posteriorly, spine-shaped or lobate; no inner corner; median dorsal canal joining smoothly posterior supraorbital canal at level of pineal organ, and converging posteriorly with opposite one to form U-shaped trajectory; only 3 lateral transverse canals extending from lateral dorsal canal; 6 pairs of branchial fossae; strong size variation of polygonal, flat-topping tubercles; dermal ring encircling median dorsal opening and orbital openings.

Remarks *Eugaleaspis xiushanensis* (Liu, 1983) was described from the Huixingshao Formation (early Wenlock, Silurian) of Xiushan, Chongqing, and used to represent the earliest occurrence of the genus *Eugaleaspis* (Liu, 1965, 1975). By comparison, the type species (*Eugaleaspis changi*) and the other referred species (*E. xijiachongensis*, *E. lianhuanensis*) were exclusively known from the Lower Devonian (Liu Y H, 1965, 1975; Liu S F, 1986). The re-examination of the holotype of *Eugaleaspis xiushanensis* (IVPP V 6793.1) suggests that this assignment is weakly supported. Unlike *Eugaleaspis changi* and *E. xijiachongensis*, in which the corner extends posterolaterally, the cephalic shield is obviously broader than long (breadth/length ratio larger than 1.4), and the posterior end of median dorsal opening anterior to the level of the posterior margin of orbits, *E. xiushanensis* has a pair of posteriorly extending corners, the cephalic shield with its breadth/length ratio smaller than 1.1, and the median dorsal opening which is more posteriorly extended. In all these regards, *E. xiushanensis* is more suggestive of *Dunyu longiforus* sp. nov. than the Devonian *Eugaleaspis* species, and is thus re-assigned to the new genus *Dunyu*.

Dunyu longiforus sp. nov.

(Figs. 1, 2A)

Etymology From *longi* (Latin), long, *forus* (Latin), opening, in reference to the long slit-like median dorsal opening.

Holotype IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing) V 17681, a complete cephalic shield.

Locality and horizon Late Ludlow, Silurian, Kuant Formation; Qujing, Yunnan, China.

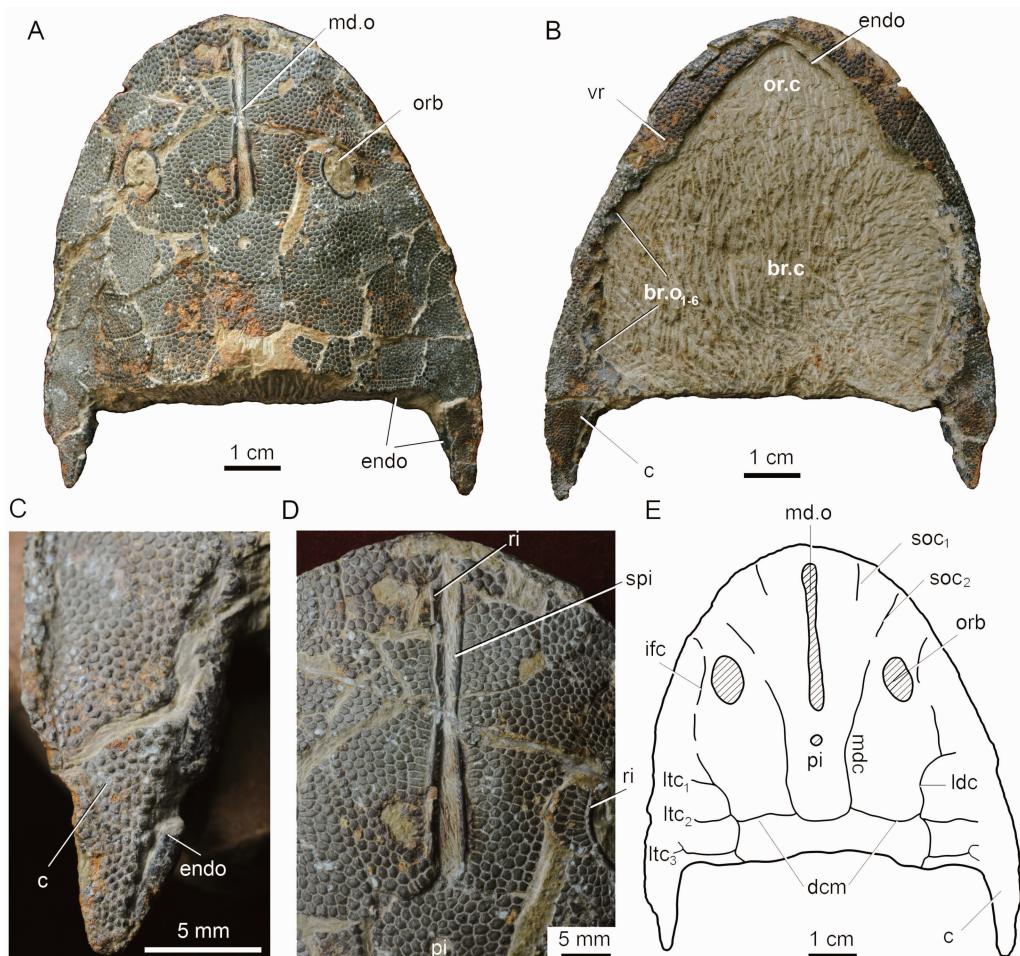


Fig. 1 Cephalic shield of *Dunyu longiforus* gen. et sp. nov., holotype IVPP V 17681
A. dorsal view; B. ventral view; C. close-up view of the left corner; D. close-up view to show the regional variation of polygonal tubercles, and minute spines on the inner surface of the dermal rim encircling the median dorsal opening; E. illustrative drawing in dorsal view

Abbreviations: br. c. branchial chamber 鳃囊; br. o₁₋₆. first to sixth branchial opening 第1至第6鳃孔; c. corner 角; dcm. dorsal commissure 背联络管; endo. endoskeleton 内骨骼; ifc. infraorbital canal 眶下管; ldc. lateral dorsal canal 侧背管; ltc₁₋₃. first to third lateral transverse canal 第1至第3侧横管; mdc. median dorsal canal 中背管; md. o. median dorsal opening 中背孔; orb. orbital opening 眶孔; or. c. oral chamber 口室; pi. pineal opening 松果孔; ri. dermal rim encircling median dorsal opening or orbital opening 中背孔或眶孔的膜质环; soc₁. anterior supraorbital canal 前眶上管; soc₂. posterior supraorbital canal 后眶上管; spi. spine-like ridge on the dermal rim of median dorsal opening 中背孔膜质环上的刺脊; vr. ventral rim of cephalic shield 头甲腹环

Diagnosis Medium-sized cephalic shield with maximum length of 85.0 mm and maximum width of 78.0 mm; corner spine-shaped; orbits anteriorly positioned, with length ratio between preorbital and postorbital portions of shield less than 0.75; third lateral transverse canal with dichotomous end; large polygonal, flat-topping tubercles with length over 2.0 mm.

Description The type specimen (IVPP V 17681) is a three-dimensionally preserved cephalic shield, with few endoskeletal elements attached. The shield has its maximum length of 85 mm, the midline length of 66 mm, and the maximum breadth of 78 mm, with a size approaching *Eugaleaspis xijiachongensis* (Liu, 1975). The breadth/length ratio of the cephalic shield is about 0.92, being distinct from those in *Eugaleaspis changi* and *E. xijiachongensis*, which are about 1.45 and 1.49 respectively. A pair of spine-shaped corners (c, Fig. 1) extends posteriorly, and leaves the maximum breadth of the shield at a level anterior to the corner apex as in *Yunnanogaleaspis* (Pan and Wang, 1980). By comparison, *Eugaleaspis* is characterized by its posterolaterally extending corners which leave the maximum breadth of the shield at a level of the corner apex.

In dorsal view, the cephalic shield is gently arched to form a domed structure with its highest point at the middle of the posterior margin. The relatively large orbital openings (orb, Fig. 1A) are oval in shape, with their maximum length up to 10 mm, and are anteriorly positioned. If we use the middle of the orbital opening as a reference point and take no account of corners, the preorbital and postorbital portions of the cephalic shield are about 28.0 mm and 38.0 mm in length respectively. The length ratio between preorbital and postorbital portions is about 0.74. In *Eugaleaspis changi* and *E. xijiachongensis*, this ratio is more than 0.9.

The median dorsal opening (md. o, Fig. 1A, D, E) is longitudinal slit-like as in other eugaleaspids. Its length is about 30.5 mm, whereas its width ranges from 1.6 to 2.5 mm, corresponding to subparallel or slightly concave lateral margins. The median dorsal opening extends posteriorly past the level of orbits. In other eugaleaspids (excluding *Eugaleaspis xiushanensis*), the posterior end of the median dorsal opening is anterior to the posterior end of the orbital opening. The median dorsal opening is encircled by a dermal ring-like structure (ri, Fig. 1D), which bears anteriorly-tapering spine-like ridges (spi, Fig. 1D) along its medial surface, suggesting the water flow through it. The similar dermal ring encircling the orbital opening bears a smooth surface medially. The pineal opening (pi, Fig. 1A, D, E) is situated immediately behind the median dorsal opening. It is round and relatively large with a diameter of 2.0 mm.

The well-preserved sensory canal system displays a unique eugaleaspid pattern (Liu Y H, 1986; Zhu, 1992). The anterior supraorbital canal (soc₁, Fig. 1E) runs from the anterior margin of the cephalic shield, and does not connect with the posterior supraorbital canal (soc₂, Fig. 1E). The median dorsal canal (mdc, Fig. 1E) joins smoothly the posterior supraorbital canal at the level of pineal opening, and posteriorly converges with the opposite one to form a U-shaped trajectory. Only one dorsal commissure (dcm, Fig. 1E) is present to connect the median dorsal and lateral dorsal canals. Three lateral transverse canals (ltc₁₋₃, Fig. 1E) extend laterally from the lateral dorsal canal. The third lateral transverse canal (ltc₃, Fig. 1E) bears a dichotomous end.

The dorsal part of the cephalic shield is flexed ventrally to form a ventral rim (vr, Fig. 1B), which encloses a large pear-shaped cavity for the oralbranchial chamber, the oral chamber (or. c, Fig. 1B) anteriorly and the branchial chamber (br. c, Fig. 1B) posteriorly. The ventral rim protrudes posteriorly to form the base of corner, and medially to form a short rod enclosing the trunk of the body. Starting from the oral margin, the ventral rim gets broader till the boundary between the oral and branchial chambers. In the branchial region, the ventral rim is narrowest at the level of the second branchial fossa, and gradually becomes wider to the level of the last branchial fossa. The part of the ventral rim contributing to branchial openings is very narrow, in contrast to the condition in *Eugaleaspis xijiachongensis* (Liu, 1975, fig. 3). Along the margin of the branchial chamber, six notches for the external branchial opening (br. o₁₋₆,

Fig. 1B) are discernable as in other eugaleaspidiforms. Few endoskeletal elements, including an arching line immediately behind the dermal oral margin (endo, Fig. 1B) and some at the postbranchial region (endo, Fig. 1A-C), are preserved in the holotype. The endoskeletal elements in postbranchial region suggest that the oralobranchial chamber is probably closed by a postbranchial wall as in *Changxingaspis* and *Meishanaspis* (Wang, 1991).

The exoskeleton is ornamented with closely set, polygonal, flat-topping tubercles. The tubercles are tesserae-like in surface view, but each of them is basally continuous with the neighboring tubercles, corroborated by fragmentary sections in the shield. The tubercles show strong size and shape variation in different regions of the cephalic shield. Dorsally, on the portion between the lateral dorsal canals or around the median dorsal opening, the tubercles are relatively large with the maximum length exceeding 2 mm (about 80 tubercles per square centimeter, Fig. 1D). By comparison, the tubercles on the corner or its neighboring areas are small (about 600 tubercles per square centimeter, Fig. 1C). Ventrally, the tubercles on the part of the ventral rim lateral to the oral chamber are evidently larger than those behind it. The similar size variation of tubercles is also present in *Eugaleaspis changi* (personal observation). The tubercles, either large or small, are usually irregular pentagonal in shape, however, the tubercles close to the median dorsal opening and orbital openings tend to be elongated, with their longitudinal axis perpendicular to the dermal ring. Sometimes, the closely set tubercles are interrupted by the sensory canals which run through between exo- and endoskeleton.

3 Discussion

Among 4 species referred to *Eugaleaspis*, *E. lianhuanensis* (Liu S F, 1986) from the Lower Devonian of Guangxi is poorly known due to the specimen preservation. Among the rest, *E. xiushanensis* from the Huixingshao Formation (early Wenlock, Silurian) of Xiushan, Chongqing (Liu, 1983) was distinguishable from the other *Eugaleaspis* species (as well as from the eugaleaspid genera) in its assumed 4 pairs of lateral transverse canals running from the lateral dorsal canal. However, Liu Y H (1986) suggested only 3 pairs of lateral transverse canals in *E. xiushanensis* yet provided no illustration or interpretation. Our new examination of the holotype (IVPP V 6793.1) of *E. xiushanensis* (Fig. 2B, 3) not only confirms Liu Y H (1986)'s observation on the sensory canal system, but also shows the striking differences between *E. xiushanensis* and the Devonian *Eugaleaspis* species, such as the corner projecting direction and the breadth/length ratio of the shield. Liu (1983) restored the corners in V 6793.1 following the condition in *Eugaleaspis changi* and *E. xuiachongensis*. The scrutiny on V 6793.1, however, shows that more parts of the cephalic shield are present behind the assumed 'corners'

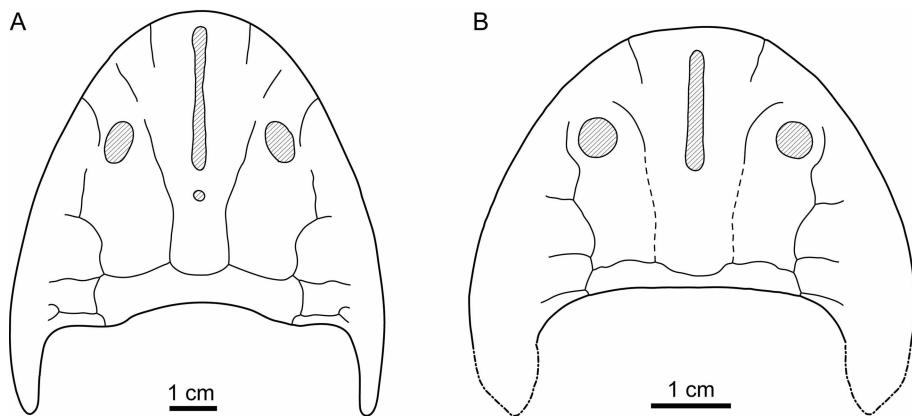


Fig. 2 Restoration of two *Dunyu* species: *D. longiforus* gen. et sp. nov. (A) and *D. xiushanensis* (Liu, 1983) (B)

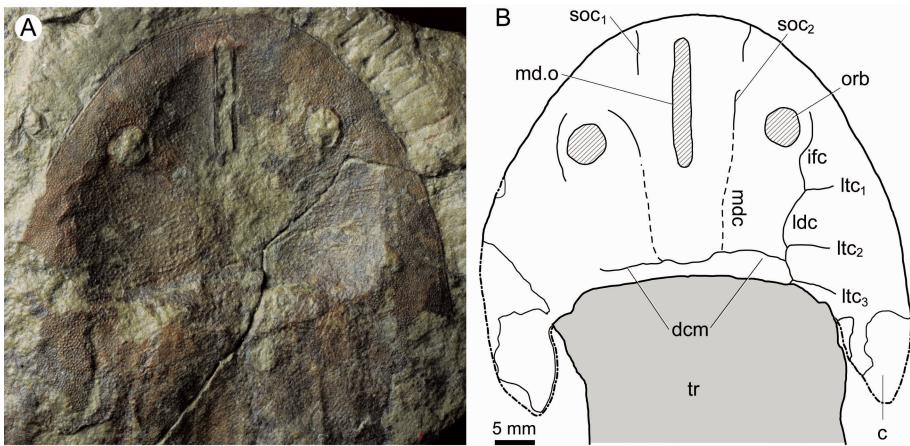


Fig. 3 *Dunyu xiushanensis* (Liu, 1983), holotype IVPP V 6793.1

A. photo showing the details of the cephalic shield; B. illustrative drawing For abbreviations see Fig. 1 plus tr. trunk squamation 躯干鳞列

(Liu, 1983). On the right side of the cephalic shield (left side on the external mould), the part behind the assumed ‘corner’ exhibits a lobate shape, although it is not completely preserved. Based on our revised restoration (Fig. 2B), *E. xiushanensis* bears a corner, which is distinguishable from that in the Devonian *Eugaleaspis* species. With posteriorly extending corners, the cephalic shield of *E. xiushanensis* looks obviously narrower than that of other *Eugaleaspis* species. In this case, if we still assign *E. xiushanensis* to *Eugaleaspis*, the diagnosis of the genus will be modified to a large extent. Alternatively, *E. xiushanensis* could be excluded from *Eugaleaspis* to keep the original diagnosis (Liu, 1965, 1980).

The discovery of the new form from the Xiaoxiang Vertebrate Fauna might provide new thread into this taxonomic puzzle. In overall, the new form resembles *E. xiushanensis* in many aspects, such as the posteriorly extending corner and the breadth/length ratio of cephalic shield less than 1.1. However, compared with *E. xiushanensis*, the new form morphologically deviates more from the Devonian *Eugaleaspis* species. If we continue to assign this new form to *Eugaleaspis*, the diagnosis of the genus has to be further modified to cover a larger morphospace (e.g. the breadth/length ratio of cephalic shield ranging from 0.9 to 1.5). In this case, a new genus (*Dunyu* gen. nov.) encompassing the new form and *E. xiushanensis* is a reasonable treatment to maintain the diagnostic stability of *Eugaleaspis*, which is the first genus of the Galeaspida described in the literature (Liu, 1965, 1980). Among the Eugaleaspidae (Liu, 1965, 1980), *Dunyu* is more closely related to *Eugaleaspis* than either to other genera (Pan and Wang, 1980; Zhu, 1992) by the absence of inner corners.

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References

Gai Z K, Donoghue P C J, Zhu M et al., 2011. Fossil jawless fish from China foreshadows early jawed vertebrate anatomy. *Nature*, **476**: 324–327

Gai Z K(盖志琨), Zhu M(朱敏), 2005. A new genus of eugaleaspids (Galeaspida, Agnatha) from the Silurian of Anji, Zhejiang, China. *Vert PalAsiat(古脊椎动物学报)*, **43**(3): 165–174 (in Chinese with English summary)

Gai Z K(盖志琨), Zhu M(朱敏), Zhao W J(赵文金), 2005. New material of eugaleaspids from the Silurian of Changxing, Zhejiang, China, with a discussion on the eugaleaspid phylogeny. *Vert PalAsiat(古脊椎动物学报)*, **43**(1): 61–75 (in Chinese with English summary)

Halstead L B, Liu Y H, P'an K, 1979. Agnathans from the Devonian of China. *Nature*, **282**: 831–833

Janvier P, 1984. The relationships of the Osteostraci and Galeaspida. *J Vert Paleont*, **4**(3): 344–358

Liu S F(刘时藩), 1983. Agnatha from Sichuan, China. *Vert PalAsiat(古脊椎动物学报)*, **21**(2): 97–102 (in Chinese with English summary)

Liu S F(刘时藩), 1986. Fossil eugaleaspid from Guangxi. *Vert PalAsiat(古脊椎动物学报)*, **24**(1): 1–9 (in Chinese with English summary)

Liu Y H(刘玉海), 1965. New Devonian agnathans from Yunnan. *Vert PalAsiat(古脊椎动物学报)*, **9**(2): 125–134 (in Chinese with English summary)

Liu Y H(刘玉海), 1975. Lower Devonian agnathans from Yunnan and Sichuan. *Vert PalAsiat(古脊椎动物学报)*, **13**(4): 202–216 (in Chinese with English summary)

Liu Y H(刘玉海), 1980. A nomenclatural note on *Eugaleaspis* for *Galeaspis* Liu, 1965; *Eugaleaspidae* for *Galeaspidae* Liu, 1965; *Eugaleaspiformes* for *Galeaspiformes* Liu, 1965. *Vert PalAsiat(古脊椎动物学报)*, **18**(3): 256 (in Chinese and English)

Liu Y H(刘玉海), 1986. The sensory system of Galeasida. *Vert PalAsiat(古脊椎动物学报)*, **24**(4): 245–259 (in Chinese with English summary)

Pan J, 1992. New galeaspids (Agnatha) from the Silurian and Devonian of China. Beijing: Geological Publishing House. 1–77

Pan J(潘江), Wang S T(王士涛), 1980. New finding of Galeaspiformes in South China. *Acta Palaeont Sin(古生物学报)*, **19**(1): 1–7 (in Chinese with English summary)

Qiao T(乔妥), Zhu M(朱敏), 2010. Cranial morphology of the Silurian sarcopterygian *Guizy unoiros* (Gnathostomata: Osteichthyes). *Sci China Earth Sci(中国科学:地球科学)*, **40**(9): 1191–1203 (in Chinese)

Qu Q M, Zhu M, Zhao W J, 2010. Silurian atmospheric O₂ changes and the early radiation of gnathostomes. *Palaeoworld*, **19**(1–2): 146–159

Tarolo L B H, 1967. Agnatha. In: Harland W B, Holland C H, House M R et al. eds. *The Fossil Record*. London: The Geological Society of London. 629–636

Wang N Z, 1991. Two new galeaspids (jawless craniates) from Zhejiang Province, China, with a discussion of galeaspid-gnathostome relationships. In: Chang M M, Liu Y H, Zhang G R eds. *Early Vertebrates and Related Problems in Evolutionary Biology*. Beijing: Science Press. 41–65

Zhao W J, Zhu M, 2010. Siluro-Devonian vertebrate biostratigraphy and biogeography of China. *Palaeoworld*, **19**(1–2): 4–26

Zhu M(朱敏), 1992. Two new eugaleaspids, with a discussion on eugaleaspid phylogeny. *Vert PalAsiat(古脊椎动物学报)*, **30**(3): 169–184 (in Chinese with English summary)

Zhu M(朱敏), Gai Z K(盖志琨), 2006. Phylogenetic relationships of galeaspids (Agnatha). *Vert PalAsiat(古脊椎动物学报)*, **44**(1): 1–27

Zhu M, Zhao W J, Jia L T et al., 2009. The oldest articulated osteichthyan reveals mosaic gnathostome characters. *Nature*, **458**: 469–473